

Mustela frenata.

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Mustela frenata Lichtenstein, 1831

Long-tailed Weasel

Mustela brasiliensis Sewastianoff, 1813:pl. 4. Type locality not given, but presumed to be Brazil. Type assumed by Merriam (1896:28) to have come from Mexico. Name preoccupied by *Mustela brasiliensis* Gmelin, 1788, an otter.

Mustela frenata Lichtenstein, 1831:pl. 42 (and accompanying unnumbered page of text). Type locality "Nähe von Mexico" [Ciudad Mexico, Mexico].

Mustela longicauda Bonaparte, 1838:38. Type locality "North America." Based on the longer-tailed "variety" of *M. erminea* reported by Richardson (1829:47) from Carlton House, Saskatchewan, Canada, which is the restricted type locality.

Putorius noveboracensis Emmons, 1840:45. Type locality not stated, but presumed to be Massachusetts (Bangs, 1896:15). Type locality restricted by Hall (1951:222) to "Williamstown, Berkshire Co., Massachusetts."

Mustela fusca Audubon and Bachman, 1843:118. Type locality "Long Island, New York."

Mustela xanthogenys Gray, 1843:118. Type locality "California." Type locality erroneously restricted to "Southern California, probably vicinity of San Diego," by Merriam (1896:25); redefined as "from the bank of Sacramento River below mouth of Feather River, or from north shore of San Francisco Bay, California," by Hall (1951:315, 317-319).

Mustela agilis Tschudi, 1844:110. Type locality "kalten, öden Hochebenen der Cordillera" [Peru].

Putorius agilis Audubon and Bachman, 1853:184. Type locality "northern part of New York." Not *Mustela agilis* Tschudi (see above).

Mustela aureoventris Gray, 1864:55. Type locality "Quito" [Pichincha, Ecuador].

Mustela macrura Taczanowski, 1874:311. Type locality "environs du lac Junin (Pérou [Peru] central)."

Mustela affinis Gray, 1874:375. Type locality "New Granada"; restricted by J. A. Allen (1916) to vicinity of Bogota, Columbia.

[*Putorius* (*Gale*) *brasiliensis*] *aequatorialis* Coues, 1877:142. Replacement name for *Mustela aureoventris* Gray, 1864, which Coues believed to be preoccupied by *Mustela auriventer* Hodgson, 1841 (a nomen nudum).

Mustela jelskii Taczanowski, 1881:647. Type locality "Cutervo" [Cajamarca, Peru].

Putorius arizonensis Mearns, 1891:235. Type locality "San Francisco Forest, Yavapai County, Arizona."

Putorius peninsulae Rhoads, 1894:152. Type locality "Hudson's, 14 miles north of Tarpon Springs" [Pasco Co., Florida].

Putorius washingtoni Merriam, 1896:18. Type locality "Trout Lake, base of Mount Adams" [Skamania Co., Washington].

Putorius saturatus Merriam, 1896:21. Type locality "Siskiyou, near southern boundary of Oregon (altitude, about 4,000 feet)" [Jackson Co., Oregon].

Putorius alleni Merriam, 1896:24. Type locality "Custer [Custer Co.], Black Hills, South Dakota."

Putorius tropicalis Merriam, 1896:30. Type locality "Jico, Veracruz, Mexico."

Putorius occisor Bangs, 1899a:54. Type locality "Bucksport [Hancock Co.—Hall, 1936:104], Maine."

Putorius macrophonus Elliot, 1905:235. Type locality "Achotal, Veracruz, Mexico."

Putorius gracilis Brown, 1908:182. Type locality "Conard Fissure" [4 mi. W of Willcockson, 15 mi. S of Harrison, Newton Co., Arkansas], Pleistocene.

Mustela costaricensis Goldman, 1912:9. Type locality "San José," San José, Costa Rica.

Mustela primulina Jackson, 1913:123. Type locality "5 miles northeast of Avilla, Jasper County, Missouri."

Mustela meridana Hollister, 1914:143. Type locality "Sierra de Merida (1630 m), near Merida, Venezuela."

CONTEXT AND CONTENT. Order Carnivora, Family Mustelidae, Subfamily Mustelinae, Genus *Mustela*, Subgenus *Mustela*, with 16 species (Wozencraft, 1993). Forty two Recent and one extinct subspecies of *M. frenata* are recognized (Hall, 1951):

M. f. affinis Gray, 1874:375, see above.

M. f. agilis Tschudi, 1844:110, see above.

M. f. alleni (Merriam, 1896:24), see above.

M. f. alifrontalis Hall, 1936:94. Type locality "Tillamook, Tillamook County, Oregon."

M. f. arizonensis (Mearns, 1891:235), see above.

M. f. arthuri Hall, 1927:193. Type locality "Remy, St. James Parish, Louisiana."

M. f. aureoventris Gray, 1864:55, see above (*aequatorialis* Coues is a synonym).

M. f. boliviensis Hall, 1938:67. Type locality "Nequejahuira, 8000 ft., Bolivia."

M. f. costaricensis Goldman, 1912:9, see above.

M. f. effera Hall, 1936:93. Type locality "Ironsides, 4000 ft., Malheur County, Oregon."

M. f. frenata Lichtenstein, 1831:pl. 42 (and accompanying unnumbered page of text), see above (*M. brasiliensis* Sevestianoff is a synonym).

M. f. goldmani (Merriam, 1896:28). Type locality "Pinabete, Chiapas, Mexico."



FIG. 1. *Mustela frenata nevadensis* from Wyoming, in summer pelage. Photograph by Steven R. Sheffield.

- M. f. gracilis* (Brown, 1908:182), see above.
M. f. helleri Hall, 1935:143. Type locality "3000 feet, Hacienda San Antonio, Rio Chinchao, Perú."
M. f. inyoensis Hall, 1936:99. Type locality "Carl Walter's Ranch, 2 miles N Independence, Inyo County, California."
M. f. latirostra Hall, 1936:96. Type locality "San Diego, San Diego County, California."
M. f. leucoparia (Merriam, 1896:29). Type locality "Pátzcuaro, Michoacan, Mexico."
M. f. longicauda Bonaparte, 1838:38, see above.
M. f. macrophonus (Elliot, 1905:235), see above.
M. f. macrura Taczanowski, 1874:311, see above (*jelskii* Taczanowski is a synonym).
M. f. meridana Hollister, 1914:143, see above.
M. f. munda (Bangs, 1899a:56). Type locality "Point Reyes, Marin Co., California."
M. f. neomexicana (Barber and Cockerell, 1898:189). Type locality "Shore of Armstrong's Lake, Mesilla" [Mesilla Park, Dona Ana County, New Mexico—Hall, 1951:333].
M. f. nevadensis Hall, 1936:91. Type locality "three miles east Baker, White Pine County, Nevada."
M. f. nicaraguae Allen, 1916:100. Type locality "Matagalpa, Nicaragua, altitude 2000 feet."
M. f. nigriauris Hall, 1936:95. Type locality "2 1/2 miles E Santa Cruz, Santa Cruz County, California."
M. f. noveboracensis (Emmons, 1840:45), see above (*Putorius noveboracensis notius* Bangs, 1899a, type locality "Weaverville, Buncombe Co., North Carolina"; *M. fusca* Audubon and Bachman, 1842 and *Putorius agilis* Audubon and Bachman, 1853, are synonyms).
M. f. occisor (Bangs, 1899a:54), see above.
M. f. olivacea Howell, 1913:139. Type locality "Autaugaville, Alabama." [Autauga County, Alabama—Hall, 1951:244].
M. f. oregonensis (Merriam, 1896:25). Type locality "Grants Pass, Rogue River Valley [Josephine County—Hall, 1951:304], Oregon."
M. f. oribus (Bangs, 1899b:81). Type locality "source of Kettle River, British Columbia, altitude 7500 feet" [the summit between the middle fork of the Kettle River and Cherry Creek at Pinnacles—Hall, 1951:270].
M. f. panamensis Hall, 1932:139. Type locality "Rio Indio, Canal Zone, near Gatun, Panama."
M. f. peninsulae (Rhoads, 1894:152), see above.
M. f. perda (Merriam, 1902:67). Type locality "Teapa, Tabasco, Mexico."
M. f. perotae Hall, 1936:100. Type locality "12500 feet, Cofre de Perote, Veracruz, Mexico."
M. f. primulina Jackson, 1913:123, see above.
M. f. pulchra Hall, 1936:98. Type locality "Buttonwillow, Kern County, California."
M. f. saturatus (Merriam, 1896:21), see above.
M. f. spadix (Bangs, 1896:8). Type locality "Fort Snelling, Minnesota" [Hennepin County, Minnesota—Hall, 1951:252].
M. f. texensis Hall, 1936:99. Type locality "Kerr County, Texas."
M. f. tropicalis (Merriam, 1896:30), see above.
M. f. washingtoni (Merriam, 1896:18), see above.
M. f. xanthogenys (Gray, 1843:118), see above.

DIAGNOSIS. *Mustela frenata* is smaller than the mink (*M. vison*), with a total length of 300–550 mm compared with 490–720 mm for *M. vison*. In summer pelage *M. frenata* has a light brown dorsum and a sharply contrasting light-colored venter extending from chin to the inguinal region, whereas *M. vison* has a uniform brown pelage with occasional ventral white spots. In *M. frenata*, the length of the upper toothrows is <20 and <17.8 mm in males and females, respectively, whereas in *M. vison* it is >20 and >17.8 mm in males and females, respectively (Hall, 1981).

Mustela frenata is larger than *M. erminea* and *M. nivalis* with little or no overlap in total length (190–340 mm for *M. erminea*, and <250 mm for *M. nivalis*). In instances where total length measurements overlap, *M. frenata* can be distinguished from *M. nivalis* by its black-tipped tail, which is longer (≥ 254 mm). *M. frenata* can be separated from *M. erminea* by its relatively longer tail, which is >44% of the total length. Skulls of male and female *M. frenata* have postglenoid lengths <46% and <47%, respectively, of the condylobasal length, whereas *M. erminea* and *M. nivalis* have postglenoid lengths >46% for males and >48% for

females (Hall, 1981). In South America, *M. frenata* differs from *M. africana* by lacking a thenar pad on the forefoot, having facial vibrissae reaching the posterior margin of the ear, the presence of the p2, and by possessing rounded tympanic bullae (Hall, 1951; Izor and de la Torre, 1978). *M. frenata* differs from the other South American weasel *M. felipei* by wider and anteriorly more flared nasals and having fur on the bottom of all feet. In addition, the three equidistant distal processes of the *M. felipei* baculum are unique within the genus and therefore distinguishable from *M. frenata* (Izor and de la Torre, 1978).

GENERAL CHARACTERS. The long-tailed weasel exhibits the typical mustelid body form with a long tail that is 44–70% of the length of head and body. The elongate body has short legs, a long neck, and a dorso-ventrally compressed triangular head. The ears are rounded and vibrissae are long (Fig. 1). Northern subspecies have a white winter pelage; southern subspecies lack a white winter coat, but have the characteristic brown dorsum all year. There is an east-west zone across North America where both the brown and white winter pelages are found. In addition, subspecies inhabiting the southwestern United States, Florida, Mexico, and Central America, have distinctive white or yellowish facial markings. Light-colored underparts, in summer pelage, extend from the chin to the inguinal region, with lateral margins tinged with buff or yellow. All subspecies have a distinctive, bushy, black tip on the tail. The extent of color on the head and intensity of pelage color in *M. frenata* varies markedly with climate, with individuals inhabiting regions of heavy rainfall having a more intense and extensive brown pelage than those in other regions. The cranium has a long braincase, greatly inflated tympanic bullae, and a palate extending beyond the M1 (Fig. 2—Hall, 1951). There is greater geographic variation in color and in the relative sizes of body parts in *M. frenata* than in *M. erminea* or *M. nivalis* (Fagerstone, 1987; Hall, 1951).

In North America, males average larger than females in external and cranial measurements (Fagerstone, 1987; Hall, 1951; King, 1989; Ralls and Harvey, 1985). Ranges of external and cranial measurements (in mm) for males and females, respectively, are as follows: total length, 330–420, 280–350; basilar length, 39–54, 35–47; length of toothrow, 14–20, 13–17; breadth of rostrum, 12–17, 10–14; interorbital breadth, 9–14, 8–12; orbitonasal length, 13–18, 12–16; mastoid breadth, 21–29, 17–25; zygomatic breadth, 24–35, 19–27; length of tympanic bulla, 12–18, 12–16; breadth of tympanic bulla, 6–10, 5–9; depth of tympanic bulla, 2–5, 2–4; length of m1, 5–7, 4–7; lateral length of P4, 5–7, 4–6; medial length of P4, 5–7, 4–6; breadth of M1, 4–5, 3–5; length of M1, 2–3, 1–3; depth of skull at basioccipital, 12–18, 10–16; depth of skull across M1–1, 10–16, 9–14 (Hall, 1951). Adult male body mass ranges between 160 and 450 g whereas females are between 80 and 250 g. Body size alone is not a reliable method of separating juvenile males from adult females; therefore a baculum or label information independently confirming sex is necessary (Johnson, 1991). Size variation in *M. frenata* is thought to reflect competitive interactions and character displacement both between male and female *M. frenata* and with *M. erminea* and *M. nivalis* (Dayan et al., 1990); however, no evidence of character displacement between any pair of North American weasel species and no correlates of size in *M. frenata* were found (Ralls and Harvey, 1985). Sexual dimorphism in skull length is not correlated with latitude, longitude, or the presence of congeners. Three geographically distinct regions of sexual dimorphism in *M. frenata* skull lengths exist in North America: a western region with small males and small females, with intermediate sexual dimorphism; a central region with large males, very large females, and low sexual dimorphism; and an eastern region with males of intermediate size, small females, and high sexual dimorphism (Ralls and Harvey, 1985). Pronounced sexual dimorphism, as well as geographic variation in the degree of sexual dimorphism, was found in condylobasal length and canine size in *M. frenata* in North America (Dayan et al., 1990).

Skull size decreases from the southern United States southward to Colombia, but from Venezuela southward there is an increase in size of skull and body mass (Hall, 1951). Skull length increases from the southern United States northward where *M. frenata* is sympatric with *M. nivalis* (Ralls and Harvey, 1985). There is a progressive decrease in inflation of the tympanic bulla from southwestern Kansas southward through the remainder of the range of *M. frenata*. There is a change in the dorsal outline of skulls in



FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of lower jaw of an adult male *Mustela frenata noveboracensis* (CUSC 2185) from Pendleton, Anderson County, South Carolina. Total length of cranium 52.1 mm. Photographs by Steven R. Sheffield.

the central United States, with specimens from Louisiana having a distinctive convexity, Missouri specimens a flattened outline, and those from North Dakota a concave outline (Hall, 1951).

DISTRIBUTION. *Mustela frenata* has the largest range of any mustelid in the western hemisphere (Fig. 3). It inhabits all life zones, from alpine to tropical, except desert. In Canada, its northern boundary is the transition between aspen parkland and the boreal forest in central British Columbia, Alberta and Saskatchewan south through southern Manitoba, Ontario, and Quebec. It has been reported from all 48 contiguous states of the United States but is absent from the Sonoran and Mojave Deserts. It is present in all Mexican states except Baja California Norte and Sur, and absent from the Sonoran life zone portions of western Sonora (Hall, 1981; King 1989). *M. frenata* is found throughout Central America, and in South America it is known from Columbia, Venezuela, Ecuador, Peru, and Bolivia (Eisenberg, 1989; Emmons and Feer, 1990; King, 1989).

FOSSIL RECORD. The long-tailed weasel has the longest stratigraphic record and widest distribution of fossils of any North American weasel (Anderson, 1984). *M. frenata* first appears in the late Blancan Borchers fauna in Kansas. It has been reported from early to late Pleistocene faunas and from Holocene faunas, from

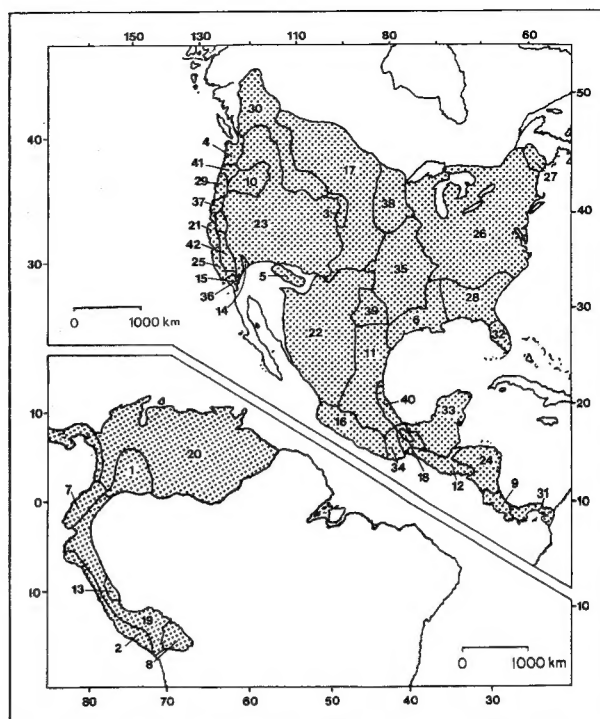


FIG. 3. Geographic range of *Mustela frenata*. Subspecies are: 1, *M. f. affinis*; 2, *M. f. agilis*; 3, *M. f. allenii*; 4, *M. f. altifrontalis*; 5, *M. f. arizonensis*; 6, *M. f. arthuri*; 7, *M. f. aureoventris*; 8, *M. f. boliviensis*; 9, *M. f. costaricensis*; 10, *M. f. efferata*; 11, *M. f. frenata*; 12, *M. f. goldmani*; 13, *M. f. helleri*; 14, *M. f. inyoensis*; 15, *M. f. latirostra*; 16, *M. f. leucoparia*; 17, *M. f. longicauda*; 18, *M. f. macrophonus*; 19, *M. f. macrura*; 20, *M. f. meridana*; 21, *M. f. munda*; 22, *M. f. neomexicana*; 23, *M. f. nevadensis*; 24, *M. f. nicaraguae*; 25, *M. f. nigriauris*; 26, *M. f. noveboracensis*; 27, *M. f. occisor*; 28, *M. f. olivacea*; 29, *M. f. oregonensis*; 30, *M. f. oribasus*; 31, *M. f. panamensis*; 32, *M. f. peninsulana*; 33, *M. f. perdus*; 34, *M. f. perotae*; 35, *M. f. primulina*; 36, *M. f. pulchra*; 37, *M. f. saturatus*; 38, *M. f. spadix*; 39, *M. f. texensis*; 40, *M. f. tropicalis*; 41, *M. f. washingtoni*; 42, *M. f. xanthogenys*. Map modified from Eisenberg (1989), Emmons and Feer (1990) and Hall (1951).

more than 30 localities in California, Colorado, Florida, Georgia, Idaho, Kansas, Maryland, Missouri, Montana, Nebraska, Nevada, New Mexico, Nueva Leon, Ohio, Tennessee, Texas, Virginia, and Wyoming (Kurtén and Anderson, 1980). An extinct subspecies, *M. f. gracilis*, was described from Conard Fissure, Arkansas, an Irvingtonian age fauna (Hall, 1936). The extinct late Pliocene mustelid, *Mustela rexroadensis*, may be ancestral to *M. frenata* (Anderson, 1984).

FORM AND FUNCTION. Populations of *M. frenata* inhabiting northern North America normally undergo two complete molts a year, with one in the autumn changing the pelage from brown to white and one in the spring reverting the pelage back to brown. In populations in southern North America, particularly in the Austral and Sonoran life zones, there are two less-pronounced seasonal pelage changes (Hall, 1951). There is no evidence indicating seasonal changes in pelage color for South American populations at higher elevations. The only portion of the pelage that does not change color during the molt is the black tip of the tail. The spring molt usually takes 20–35 days (Glover, 1942; Noback, 1935), and the autumn molt takes 37–70 days (Miller, 1931; Noback, 1935). The spring molt begins with the appearance of a few brown hairs on the nose, forehead, and between the shoulders. Then brown pelage appears at the base of the tail, developing into a mid-dorsal stripe. Brown hairs then begin to appear lateral to the mid-dorsal stripe, and on the dorsal aspect of the limb-girdle regions. These appendicular stripes progress distally to the extremity of each limb. All dorsal stripes continue to expand until the molt has been completed (Glover, 1942; Noback, 1935). The spring molt is induced by a gonad-



FIG. 4. Baculum of *Mustela frenata* (CUSC 2185) from Pendleton, Anderson County, South Carolina (lateral view). Length is 26 mm. Photograph by Steven R. Sheffield.

otrophic hormone (Wright, 1950). Individual guard hairs have narrow proximal diameters ($<49\ \mu\text{m}$) but are at least 1.5 times wider distally (Short, 1978). The guard hairs have elongate and petal-like cuticular scales. Females possess five pair of abdominal inguinal mammae that are not bilaterally symmetric in placement (Hall, 1951).

The skeleton of *M. frenata* is typical of weasels with a long, slender, and low body form. The vertebral formula is 7C, 14–15 T, 5–6 L, 2–3 S, and 19–23 Ca, total 47–54 (Hall, 1951). The baculum develops a distinctive proximal head at sexual maturity (Fig. 4—Wright, 1951).

The dental formula is $i\ 3/3$, $c\ 1/1$, $p\ 3/3$ and $m\ 1/2$, total 34. The absence of the primitive first and second premolars, resulting in a slight shortening of the face and lengthening of the third and fourth premolars, is thought to be an adaptation for a carnivorous diet. The deciduous dentition is composed of one canine and three cheek-teeth (premolars) on each side of the upper and lower jaws (Hall, 1951).

Of the two forms of hemoglobin found in *M. frenata*, one—like that found in all members of the family Mustelidae—is identical to that of other groups of the superfamily Canoidea. However, all mustelids exhibit a second and equally prevalent major form of hemoglobin, as do some procyonids (Seal, 1969).

Metabolic rate is inversely related to ambient temperature, with males having a greater metabolic rate (mean $\pm 1\ SD$ is $1.36 \pm 0.20\ \text{kcal/h}$) than females ($0.84 \pm 0.12\ \text{kcal/h}$). Because of its long, slender shape, *M. frenata* assumes a flattened, disk-like and coiled posture when resting, which results in considerably more exposed surface area than would a sphere of the same mass. The relatively higher metabolic rate and mass specific rate of heat loss, compared with less slender mammals of similar mass, is attributed to the high ratio of body surface-to-volume and the shorter fur (Brown and Lasiewski, 1972).

The average daily food requirement for captive *M. frenata* is about 1.5 voles/day (Powell, 1973). Captive adult *M. frenata* consume 17–33% of their body weight in 24 h, but growing young can consume more (DeVan, 1982; Hamilton, 1933; Sanderson, 1949). Captive *M. frenata* (5–7 weeks old, 8–10 weeks old, and adult) consumed 22%, 24% and 18%, respectively, of their body mass each day, but at times the young consumed up to 40% of their body mass in 24 h (Sanderson, 1949). Food consumption probably is higher in wild *M. frenata* (Fagerstone, 1987).

ONTOGENY AND REPRODUCTION. Fertilization usually occurs 53–80 h after copulation. Females exhibit a lengthy period of delayed implantation beginning around 68 days post-coitus and lasting until day 251. Following implantation, all post-blastocyst stages of development occur within 27 days (King, 1989; Wright, 1948a).

In North America, the average gestation period, including delayed implantation, is 279 days, with a range of 205–337 days. The gestation period for tropical and other South American *M. frenata* is not known. Temperate Nearctic female *M. frenata* give birth to one litter of 4–5 young annually, with a maximum of nine young, between mid-April and early May (Fagerstone, 1987; Hamilton, 1933; Wright, 1942). Parturition consists of four basic activities by the female: resting; moving about the nest; labor, characterized by uncontrollable and violent muscular contractions; and care of the newborn, such as licking and placement of young within the ventral

curvature of the female's thoracic and abdominal regions. The total time span for these activities is 6 min for each birth. Lactation begins soon after parturition and lasts up to 5 weeks (DeVan, 1982).

Onset of the estrous cycle is influenced by reproductive history, and varies geographically. Females that had a litter the previous spring enter estrus 39–104 days postpartum, whereas others enter estrus as early as mid-March. The estrous cycle in southern populations averages longer than in northern populations due to the earlier date of onset in southern populations (DeVan, 1982). Females generally mate early in their first summer (Wright, 1948a) with the adult male that holds the territory where their mother resides. Due to high turnover of resident males, this male is not likely to be the same one that bred with their mother (Fagerstone, 1987). Males are sexually immature during their first summer and first breed at 15 months of age (Wright, 1947). Adult males are sexually active as early as February and remain so until as late as December. As with females, there are geographic differences in the male reproductive cycle, but the difference is in the time of cessation, with northern males becoming sexually inactive by September. Maximum size of testes occurs in August. Estrous females remain receptive for 3–4 days, during which they have a swollen vulva. Coitus usually is lengthy, lasting up to 3–4 h (Wright, 1948b).

The young are born blind and have only a few long, white hairs (Hamilton, 1933). At approximately 2 days of age, the young are covered by a fine, long, white pelage that does not completely conceal the skin, and the pinnae remain folded. At 1 week of age, the young are covered with fuzzy white hairs of uniform length that obscure all but the venter. At this age the sexes are similar in appearance, and have an average mass of ca. 8 g. At 2 weeks, there is an extensive coat of white hairs, with those on the head, neck, and shoulders longer than those on the back. The ears are slightly pigmented at this time, and none of the teeth has protruded through the gums. Males are larger than females, having an average mass of 17 g and an average length of 100 mm, whereas females average 14 g and 89 mm. Both sexes are able to support themselves on their legs, but males can crawl better than females. At 3 weeks, the young are well-furred dorsally with the pelage becoming gray. There is a sharp color line separating the fur of the back from that on the side. The tip of the tail is black, and there are fleshy protuberances in the mystacial and superciliary areas. The average mass of males is 27 g and total length is 150 mm; average mass of females is 21 g and total length is 127 mm. At this age, the young are capable of agile crawling. The deciduous canine and premolars have erupted. At 3.5 weeks, the incisors begin to protrude through the gums. At 4 weeks, males average 39 g and 211 mm in total length, whereas females average 31 g and 196 mm in total length. At 5 weeks, the young begin opening their eyes, females first, followed by males. The young begin eating meat and weaning takes place. The pelage resembles that of the adult summer pelage, but is much darker. At 6 weeks, long guard hairs appear and the average mass and length of males is 81 g and 240 mm, and for females is 62 g and 215 mm. The characteristic weasel odor has developed by 6 weeks (Sanderson, 1949). At 7 weeks, males have an average mass of 101 g—approximately equal to that of the mother—and have a darker pelage than female littermates. The females have an average mass of 73 g. The tail of both sexes becomes noticeably pointed by 2–4 months of age. Juvenile dentition persists for up to 11 weeks of age, at which time the adult dentition begins to appear (Hall, 1951). The eruption sequence for adult cheek-teeth is M, P₄, P₂, P₃, and m₁, p₂, p₃, p₄, which is considered primitive among Carnivora (Slaughter et al., 1974).

Three subadult and one adult age classes for *M. frenata* were recognized by Hall (1951): juvenile, birth to 3 months; young, 3–7.5 months; subadult, 7.5–10 months; adult, >10 months. Juveniles can be distinguished by the presence of deciduous dentition, whereas the remaining two non-adult groups and the adult group are separable by the degree of closure of cranial sutures. Skull size increases from birth to ca. 6 months. The overall size of the skull does not change appreciably thereafter. There are few traces of cranial sutures in the skulls of either sex at 1 year (Hall, 1951). Adult males can be distinguished from subadults by the increased mass of the baculum at the time of first spermatogenesis: the average mass of the baculum is $<30\ \text{mg}$ prior to first spermatogenesis and $>52\ \text{mg}$ thereafter (Wright, 1947).

ECOLOGY. *Mustela frenata* is the largest and least spe-

cialized member of the small carnivore guild including *M. erminea* and *M. nivalis* that prey on small to medium-sized mammals (Rosenzweig, 1966). *M. frenata* is a generalist predator, feeding upon a wide variety of prey, and is able to switch to alternative prey when normal prey numbers are low (Gamble, 1981; King, 1989). There is some degree of dietary overlap, especially in sympatric populations of *M. frenata* and *M. erminea*, which may result in competition. The larger size of *M. frenata*, however, allows it to take a wider variety of prey than can the smaller *M. erminea* (Simms, 1979). The frequency of occurrence of a prey species in the diet varies seasonally, geographically, and by gender, with males generally taking larger prey than females (Fagerstone, 1987; King, 1989). In North America, *M. frenata* feeds upon a wide variety of small vertebrates, but concentrates on rodents and rabbits of small to medium size. When available, voles (*Microtus*, *Clethrionomys gapperi*) are more commonly consumed than other prey, but deer mice (*Peromyscus*) are also commonly taken (Hall, 1951). Other rodents less commonly preyed upon are grasshopper mice (*Onychomys*), harvest mice (*Reithrodontomys*), cotton rats (*Sigmodon*), woodrats (*Neotoma*), bog lemmings (*Synaptomys*), muskrats (*Onychomys*), round-tailed muskrats (*Neofiber alleni*), meadow jumping mice (*Zapus hudsonius*), house mice (*Mus musculus*), rats (*Rattus*), pocket gophers (*Thomomys*, *Geomys*, *Cratogeomys*), ground squirrels (*Spermophilus*), chipmunks (*Tamias*, including *Eutamias*), red squirrels (*Tamiasciurus hudsonicus*), gray squirrels (*Sciurus carolinensis*), fox squirrels (*Sciurus niger*), flying squirrels (*Glaucomys*), and mountain beavers (*Aplodontia rufa*; Fagerstone, 1987; Feldhamer and Rochelle, 1982; Gamble, 1981; Hall, 1951; King, 1989). Rabbits (*Sylvilagus*, *Romerolagus diazi*), snowshoe hares (*Lepus americanus*) and pikas (*Ochotona princeps*) are also commonly taken as prey (Cervantes-Reza, 1981; Fagerstone, 1987; Hall, 1951). Moles (*Scalopus aquaticus*, *Condylura cristata*, *Scapanus*), shrews (*Microsorex hoyi*, *Sorex*, *Blarina*), and big brown bats (*Eptesicus fuscus*) are less commonly taken (Hall, 1951; Mumford, 1969). A record of predation on newborn domestic pigs (*Sus scrofa*) exists (Polderboer, 1948). Avian prey taken by *M. frenata* includes red-winged blackbirds (*Agelaius phoeniceus*), tree sparrows (*Spizella arborea*), bobwhite quail (*Colinus virginianus*), flickers (*Colaptes auratus*), song sparrows (*Melospiza melodia*), dark-eyed juncos (*Junco hyemalis*), domestic chicken (*Gallus domesticus*), and blue-winged teal (*Anas discors*; Fagerstone, 1987; Hall, 1951). Long-tailed weasels have a particular affinity for birds' eggs and commonly will raid nests (Fleskes, 1988; Teer, 1964). Rarely taken prey are king snakes (*Lampropeltis*), bull snakes (*Pituophis*), lizards, and ground beetles, grasshoppers, and other insects. Other small carnivores such as the weasels *M. nivalis* and *M. erminea* are taken occasionally (Gamble, 1981; Polderboer et al., 1941). Commonly consumed carrion includes deer (*Odocoileus*), beaver (*Castor canadensis*), and woodchuck (*Marmota monax*; Hall, 1951). Although not well known, the diet of tropical *M. frenata* is thought to consist mainly of small mammals, rabbits, and birds and their eggs (Emmons and Feer, 1990). At Kesterson Reservoir, California, a highly contaminated agricultural area, *M. frenata* and its prey were found to have significantly elevated liver selenium levels (Clark, 1987).

The long-tailed weasel often has been considered an agricultural pest due to its predation on poultry. However, the positive role of *M. frenata* as a predator of rodent pest species far outweighs the occasional killing of domestic and game species (Polderboer et al., 1941; Quick, 1944, 1951). In Gunnison Country, Colorado, it was estimated that, in an area of 10,240 km², about 8,000 *M. frenata* inhabited the area, killing more than 30,000 small mammals per day—10,000,000 per year (Quick, 1951).

Foxes and raptors are the primary predators of long-tailed weasels (King, 1989; Latham, 1952; Powell, 1973). There is significant predation by red foxes (*Vulpes vulpes*) and gray foxes (*Urocyon cinereoargenteus*) on *M. frenata* in Pennsylvania (Latham, 1952). Raptors including great-horned owl (*Bubo virginianus*), snowy owl (*Nyctea scandiaca*), barred owl (*Strix varia*), rough-legged hawk (*Buteo lagopus*), and goshawk (*Accipiter gentilis*) prey on *M. frenata*. Coyotes (*Canis latrans*), martens (*Martes americana*), bobcats (*Lynx rufus*), domestic dogs and cats, and less frequently water moccasins (*Aghastisodon piscivorus*) and rattlesnakes (*Crotalus*) prey on *M. frenata* (Hall, 1951). A record of attempted food piracy by *M. frenata* on a snowy owl attests to their fearlessness, but may account, at least in part, for their presence in the diet of owls (Boxall, 1979). Their erratic hunting pattern and characteristic

black-tipped tail possibly serve as a means of confusing raptors and reducing predation (Powell, 1973, 1982). Other causes of mortality in *M. frenata* include Powassan virus (Main et al., 1979) and human-related mortality as a result of trapping, shooting (predator control), and automobile use.

Mustela frenata is an economically important furbearer and its pelt has been sold and traded by humans. From 1970 to 1976, an average of 43,228 *M. frenata* pelts were bought in the United States and Canada, averaging \$0.58/pelt and \$24,976.95/year (Deems and Pursley, 1978). *M. frenata* has been live-trapped successfully using Sherman, Longworth, Havahart and National live traps (Fagerstone, 1987). In a live-trapping efficacy study, significantly more long-tailed weasels were caught in double-door Havahart traps than in single-door National or single-door wooden traps (Belant, 1992). Good trap success for *M. frenata* was achieved using a combination of Havahart No. 0 (for females and small males) and No. 1 (for large males) live traps and modified National R1 box traps with holes drilled in them to prevent moisture condensation. The most efficient trap bait is freshly killed laboratory mice (DeVan, 1982).

External parasites on North American *M. frenata* include the fleas *Chaetopsylla stewarti*, *Ctenophthalmus pseudagrytes*, *Echinophaga gallinacea*, *Epetidia wenmanni*, *Diamanus montanus*, *Foxella ignota*, *Hoplopsyllus anomallus*, *Hystrichopsylla schefleri*, *Megabothris abantis*, *M. asio*, *Meringis hubbardi*, *M. parkeri*, *Monopsyllus eumolpi*, *M. wagneri*, *Nosopsyllus fasciatus*, *Orchopeas sexedentatus*, *Oropsylla idahoensis*, *Peromyscopsylla catta*, and *Polygenis gwyni* (Eads et al., 1987; Hansen, 1964; Layne, 1993; Stack, 1958; Whitaker and Goff, 1979a; Wobeser, 1966). One species of sucking louse (*Hoplopleura erratica*) and two species of biting lice, *Neotrichodectes minutus* and *N. mephitis* have been reported (Emerson, 1972; Whitaker and Goff, 1979a, 1979b). Ticks include *Amblyomma tuberculatum*, *Dermacentor andersoni*, *D. occidentalis*, *D. variabilis*, *Ixodes cookei*, *I. dammini*, *I. kingi*, *I. pacificus*, *I. rugosus*, *I. scapularis*, *I. sculptus*, *I. texanus* (Beck, 1955; Bishop and Trembley, 1945; Furman and Loomis, 1984; Layne, 1993; Morlan, 1952; Whitaker and Goff, 1979a; Wilkinson, 1984). Chiggers include *Euschoengastia peromysci* and *Eutrombicula alfreddugesi*. Mesostigmatid mites include *Androlaelaps fahrenheitsi*, *Haemogamasus liponyssoides*, *H. occidentalis*, *H. reidi*, *Laelaps multispinosa*, *Echinonyssus longichelae*, and *E. femoralis*, and astigmatid mites include *Aplodontopus sciuricola*, *Glycyohagus hylandi*, *G. hypudaei*, *Xenoryctes latiporus*, *Zibethicarus ondatrae*, *Lynxacarus mustelae*, and *L. nearcticus* (Fain and Hyland, 1974; Herrin, 1970; Whitaker and Goff, 1979a; Whitaker and Wilson, 1974). A number of flea and mite records probably are the result of predation on small mammals, because several of the reported parasites are characteristic of the parasite faunas of the prey of *M. frenata*. In plague-enzootic areas of the United States, *M. frenata* has been found to be seropositive for plague (Barnes 1982). Internal parasites reported for *M. frenata* from North America include one species of trematode (*Alaria mustelae*) and three species of parasitic nematodes (*Filaroides bronchialis*, *Molineus mustelae*, and *Skjrabingylus nasicola*; Gamble and Riewe, 1982; Goble and Cook, 1942; Johnson, 1979; Schmidt, 1965). In Manitoba, Canada, 100% of *M. frenata* were infested with *S. nasicola*, and the degree of cranial damage, host age, sex, and diet suggested paratenic hosts (Gamble and Riewe, 1982).

Mustela frenata populations are more stable than those of *M. erminea* or *M. nivalis*. This relative stability may reflect the generalist-predator niche occupied by *M. frenata*, as well as their ability to reproduce while relying on alternate prey (Gamble, 1981). However, *M. frenata* populations generally fluctuate, and they frequently become locally extinct in response to changes in prey numbers (King, 1989). There have been reports of multi-year fluctuations in an *M. frenata* population in Vermont, with weasel numbers changing possibly in response to prey abundance (Osgood, 1935). In Alberta, *M. frenata* had a 10-year cycle synchronous with that of the snowshoe hare. About 81% of the annual variation in weasel numbers, as indexed by capture rates, was attributable to fluctuations of hares, voles (*Microtus* and *Clethrionomys*) and mice (*Peromyscus*—Keith and Cary, 1991). *M. frenata* is difficult to census because of its low densities and long distance movements. Estimates of densities vary widely by habitat and prey availability (King, 1989). Reported densities of *M. frenata* range approximately from 0.004–0.008/ha in western Colorado (Quick, 1951) to 0.02–

0.18/ha in Kentucky (DeVan, 1982) to 0.19–0.38/ha in chestnut-oak forest and 0.07–0.09/ha in scrub oak-pitch pine forest in Pennsylvania (Glover, 1943), and 0.2–0.3/ha in cattail marsh in Ontario (Wobeser, 1966). Sex ratios tended to be equal in these populations. In areas of sympatry, *M. frenata* generally is less abundant than *M. erminea* (Fitzgerald, 1977).

The long-tailed weasel prefers habitats with abundant prey, such as those where dens of burrowing rodents are numerous and close to cover, supporting large populations of small mammals and birds (Polderboer et al., 1941). Prey species diversity probably is an important factor in determining suitable habitat for *M. frenata* (Gamble, 1981). *M. frenata* appears to be at least partially restricted to habitats in close proximity to standing water (Gamble, 1981; Hall, 1951; Quick, 1951). Waterways provide access to suitable habitat and are a natural avenue for dispersal in *M. frenata*, particularly in areas that otherwise are unsuitable (Fagerstone, 1987). In Pennsylvania, densities in winter are highest (0.38/ha) in habitats having a dense understory (Glover, 1943). Cattail marshes are the most commonly used habitat of long-tailed weasels in Rondeau Park, Ontario (Wobeser, 1966). Abundance is especially high in cut and slash habitats with dense sprout growth (Glover, 1943). Lateral and ecotone habitats with high prey density is selected by long-tailed weasels in Manitoba (Gamble, 1981). In Kentucky, dens are located in dense-brushy vegetation in or bordering dry creeks and drainage ravines, and foraging activities are concentrated along the borders of pasture and old fields (DeVan, 1982). When occurring in the same areas, *M. frenata* tends to hunt in forest habitats more than *M. erminea* (Fitzgerald, 1977).

Males and females live separately most of the year, but their home ranges may overlap. The home ranges of males average larger than those of females and may include home ranges of more than one female. During the breeding season, home ranges of males increase in size, allowing more frequent contact with females. There is little overlap of home ranges of males. The home range of *M. frenata* largely reflects the availability of prey. There are no significant differences in the size of winter and summer home ranges in Kentucky weasels. Summer home ranges vary from 16 to 24 ha and winter home ranges from 10 to 18 ha (DeVan, 1982). However, in areas where prey is scarce in winter, home ranges may be 80–160 ha (Quick, 1944, 1951). A smaller winter home range may reduce energy used for thermoregulation, as in winter, long-tailed weasels make a greater number of short trips than in summer. In a pattern similar to reduction of home range size in winter, the maximum distance traveled from the den decreases as prey density increases. During one excursion, a male weasel traveled approximately 983 m in July, but only traveled a maximum distance of 465 m in January and February (DeVan, 1982).

BEHAVIOR. *Mustela frenata* exhibits the highly active behavior characteristic of mustelids. It is active out of the den day and night, primarily for foraging and feeding (Griddle and Criddle, 1925; Soper, 1946). It runs in a series of bounds with the back bent during each bound. The tail is elevated during running either parallel to, or at an angle of up to 45° from the ground (Hall, 1951). *M. frenata* has a keen sense of smell and hearing. Although vision appears to be relatively poor, it has an excellent ability to detect moving objects. It detects its prey primarily by scent and hearing prior to locating it visually (Fagerstone, 1987). *M. frenata* has been observed swimming (Davis, 1944; Green, 1936; Wobeser, 1966) and often splashes or runs through the water (Pearce, 1937), and water is important to its daily activities (Gamble, 1981; Hall, 1951). *M. frenata* will readily tunnel under the snow when hunting during the winter (Fitzgerald, 1977). Long-tailed weasels readily climb trees in pursuit of prey (DeVos, 1960; Pearce, 1937). Ascent of tree trunks begins with an initial vertical leap of about 1 m followed by short spirals around the tree trunk of about 1 m/spiral (Pearce, 1937). Climbing trees may serve as an anti-predator strategy in *M. frenata* (Dekker, 1993). *M. frenata* was found to cache food in old passerine nests located in shrubs in Indiana during the winter when carcasses remain frozen (Weeks, 1991).

Predatory behavior consists of foraging, pursuit, attack, subduing, killing, and feeding activities. *M. frenata* actively hunts its territory in search of prey, searching underground, on the ground, and arboreally. They are known to hunt in snowshoe hare runways (Keith and Meslow, 1966) and pocket gopher burrows (Vaughan, 1961). Predatory behavior varies and is dependent on size of prey, whether prey is bird or mammal, and location of prey (above or

below ground or arboreal—Allen, 1938; Byrne et al., 1978; Leopold, 1937; Pearce, 1937). Above-ground foraging is characterized by a zig-zag pattern that allows the investigation of more area (Powell, 1979). They pursue rabbits at a distance of about 3 m while making repeated leaps at the prey (Leopold, 1937). These leaps result in repeated non-killing strikes that weaken large prey. Medium and small-sized prey are pursued in a more determined and rapid fashion, with one to six short dashes ending with the final attack. The means of subduing prey is determined by prey size, with large prey, such as rabbits, initially grabbed by the most convenient part of the animal. Above-ground medium-sized prey (such as ground squirrels and chipmunks) usually are subdued and killed by biting the nape of the neck, severing the spinal cord. Underground medium-sized prey are subdued and killed by a ventral attack and a grasping of the throat that results in suffocation. The suffocation method may be effective underground because it results in a short period of prey resistance (Byrne et al., 1978). Suffocation probably is not used for above-ground kills because the prey can kick the weasel more effectively. Small-sized prey, such as mice and voles, usually are subdued when the weasel throws its body into a tight coil around the prey; these prey are killed by a bite to the nape of the neck (Allen, 1938). When preying on social species, *M. frenata* may be attacked by cohorts of captured prey (Harestad, 1990). After killing their prey, *M. frenata* often licks blood from the wound. Feeding begins in the head and abdominal regions; small prey usually are entirely consumed (Pearce, 1937). *M. frenata* drinks water frequently. In captivity, they drink about 25 ml of water per day (Hamilton, 1933).

In captivity, urination generally precedes defecation with an average of 10 eliminations per 24 h period. Long-tailed weasels utilize den entrances as locations for latrines (Polderboer et al., 1941; Quick, 1944), and often deposit bones and skin in the latrine (Svilha, 1931). Feces typically are dark brown or black and long, narrow, and spiral (Hamilton, 1933). After defecation the weasel often drags its anal region over leaves for a distance of 15–30 cm (Pearce, 1937).

Resting behavior consists of periods of sleeping and wakeful but immobile periods. Long-tailed weasels are reported to lie immobile at burrow entrances for 0.5 h or more with only the head showing. During these periods, the weasel is alert to sounds, odors, and movements. *M. frenata* appears to become quiescent during hot weather. This quiescence is accompanied by a decrease in overall alertness (Pearce, 1937). Cooler night and morning temperatures allow a return to heightened activity and alertness. Nonpredatory, aggressive behavior often consists of a series of loud, high-pitched screeches, or a stamping of hind feet (Hall, 1951; Moore, 1944). A high incidence of road-killed *M. frenata* in western Washington suggests that males exhibit transient behavior during the breeding season, roaming larger areas in search of potential mates (Buchanan, 1987).

Adult *M. frenata* normally lead a solitary life except during the breeding season and while rearing young (Fagerstone, 1987; King, 1989). However, males and females may remain together for periods during the non-breeding season (Hamilton, 1933; Quick, 1944; Wobeser, 1966). Males that have previous mating experience usually mate successfully with an estrous female. Males locate receptive females by scent. Reproductive behavior in males usually begins with smelling areas where an estrous female has urinated. The male pursues the female, often with a scuffle ensuing, ending with the male grasping the female by the back of the neck with its teeth. Resistance by females varies from the emission of low-chattering noises, to vigorous and prolonged physical resistance. Once the female ceases resistance, the male clasps her lower abdomen with his forefeet and arches himself over her posterior region, with subsequent penile insertion and copulation. The mated pair will remain locked for an average of 2–3 h. Following copulation, the female attempts to break away. After mating there is varied tolerance of the male by the female, from sharing the nest to excluding him from the nest (Wright, 1948b).

The nest is often located in a burrow constructed by another animal or under rocks or brush piles (Fitzgerald, 1977; Frank and Lips, 1989; Polderboer et al., 1941; Quick, 1951; Sanderson, 1949). The nest itself usually is borrowed from a prey species and is an enlarged chamber 3.5–5.0 cm in diameter, lined with dried grass and the fur of the prey. Several burrows usually radiate from the nest and may be used as latrines or food caches (Fagerstone, 1987).

Three basic patterns of vocalizations have been described for *M. frenata* (Svendsen, 1976). A trill is the most frequent vocalization and is used during periods of calm investigation, play, and hunting. It is composed of a series of rapid short-duration, low-frequency calls averaging 0.024 s with intervals of 0.0375 s. The trill has two harmonics: 200–500 and 750–1000 Hz. A screech is utilized when the weasel is disturbed. It too is composed of two parts, with a total duration of 0.15 s and intervals of about 3 s. Screeches usually are repeated up to seven times. These calls are usually 0.35 s in duration. The screech probably serves to startle predators during a defensive or threat display, for it is often accompanied by an open-mouth gape and a sudden lunge (Svendsen, 1976). A squeal is often emitted while the animal is being handled, and is considered a distress call. Juvenile *M. frenata* show play behavior and often will chew on each other during play (Sanderson, 1949).

GENETICS. The diploid number of chromosomes in *M. frenata* is 42 and the fundamental number is 66. There are 22 pairs of metacentric and submetacentric chromosomes and 18 pairs of acrocentric autosomal chromosomes. The X and Y chromosomes are submetacentric. There commonly is a secondary constriction near the ends of the long arms of autosomal chromosome 10, with a similar but less commonly occurring constriction on autosomal chromosome 2 (Basrur, 1968). No electrophoretic or molecular genetic data are known for this species.

REMARKS. The latin word *Mustela* means weasel. The specific epithet *frenata* is derived from the Latin *fraenum* meaning bridle, referring to the bridled markings of the face (Jaeger, 1955). Most of our knowledge of this species is a result of studying individuals and populations from the United States and Canada. Very little is known about the biology of Mexican, Central American, or South American *M. frenata*. Due to the low densities and periodic fluctuations of North American *M. frenata* populations, this species is listed as endangered, threatened, rare, or as a species of special concern in many states and provinces. In Canada, *M. f. longicauda* has been listed as threatened by the Commission on the Status of Endangered Wildlife in Canada since April 1982. We thank M. J. Barrette of the Department of Biology, Fitchburg State College for typing earlier drafts of the manuscript, the Interlibrary Loan Departments at Fitchburg State College, Oklahoma State University, and Clemson University for assistance in obtaining journal articles, and S. Anderson, T. L. Best, A. L. Gardner, G. A. Heidt, and J. A. Lackey for critically evaluating earlier drafts of the manuscript.

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